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MIGRATIONS AND AFFINITIES OF THE FOSSIL PROBOSCIDEANS OF EURASIA, NORTH AND SOUTH AMERICA, AND AFRICA

(SIXTH CONTRIBUTION ON THE EVOLUTION OF THE PROBOSCIDEA)

DR. HENRY F. OSBORN
AMERICAN MUSEUM OF NATURAL HISTORY

DR. HIKOSHICHIRO MATSUMOTO, of the Tôhoku Imperial University, Sendai, Japan, has recently been studying the Fayûm collections of primitive proboscideans and hyracoids in The American Museum of Natural History, followed by a visit to the British Museum where he has been making comparisons with the types of these mammals, described by Dr. C. W. Andrews in his series of papers beginning in 1901. In 1918 Doctor Matsumoto[1] published a series of five papers on the elephants, turtles, sirenians, cervids, and bisons of Japan compared with those of India. He pointed out that the Japanese archipelago was an integral part of the continent from the beginning of the Miocene to the middle of the Pleistocene, and that the period of separation seems to have dated from the recent Pleistocene. Consequently its relations with the animal life of southern China and with the more distant peninsula of India are very close.

The ancient Japanese proboscideans are chiefly of three kinds, of which the most numerous are the forest-living stegodonts, closely related in their specific phases to the stegodonts of China, such as the species *Stegodon sinensis*. There also occurs in the early Pleistocene the great *Loxodon antiquus namadicus,* the straight-tusked elephant, which ranged all over southern Eurasia and probably arose originally in the African continent.

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[1] 1. "On a New Archetypal Fossil Elephant from Mt. Tomuro, Kaga." 2. "On a New Fossil Trionyx from Hokkaido." 3. "A Contribution to the Morphology, Palæobiology and Systematic of *Desmostylus*." 4. "On a New Archetypal Fossil Cervid from the Prov. of Mino." 5. "On Some Fossil Bisontines of Eastern Asia." *Sci. Rep. Tôhoku Imp. Univ.*, Sec. Ser. (Geology), Vol. III, No. 2.

In the early formations, such as the Middle Pliocene of Tomuro, Kaga, we meet the *Elephas auroræ,* regarded by the author as an intermediate type between the stegodonts of the Upper Pliocene of India and *Elephas planifrons,* which in turn is related to the true mammoths (*Elephas primigenius*) and wandered all over southern Europe in Upper Pliocene time, namely, Bessarabia, Austria, and southern France. In still earlier deposits, such as the Upper Miocene of Kuji, occurs a mammal which the author refers to *Stegodon latidens,* an ancestral stegodont of Burma, India. In the Lower Miocene of the Province of Mino occurs a form very similar to the *Trilophodon angustidens* of the Middle Miocene of France, ancestral to all the long-jawed proboscideans.

The *Stegodon* itself is peculiar to India, China, Japan, and the larger islands of the Malayan archipelago, such as Sumatra, Java, and Borneo. The author notes that there is a marked difference between the sexes, so that the stegodonts of each geologic period seem to have received two specific names, one applied to the female, the other to the male form. Among these couples are *S. Cliftii-bombifrons,* dating from the Upper Pliocene and from the Lower Pliocene of India; *S. ganesa-insignis,* dating from the Upper Pliocene and from the Postpliocene of the same area; *S. sinensis-orientalis,* dating from the same strata of China and Japan; *S. airawana-trigonocephalus* from the Postpliocene of Java. This sex dimorphism is very marked, especially in the great disparity of size of the upper tusks, which are much smaller and more slender in females than in males. This tusk structure in turn affects the entire form of the head.

The *Bison occidentalis* of Japan seems to spring from the *B. sivalensis* of the Upper Pliocene of India. It is similar in fact to the bison found in the ancient Pleistocene of Kansas, in the basin of the Ohio River, in Alaska, and in the region of the Yenisei River in Siberia. According to the author, in the Transbaikal region the same species occurs in association with the giant woolly rhinoceros (*Diceros antiquitatis*), with the hairy mammoth (*Elephas primigenius*), and with the heavy-horned bison (*Bison crassicornis*).

Quite a different order of distribution has the remarkable *Desmostylus*, a sirenian or sea cow peculiar to the coasts of the Pacific Ocean, first described from the California coast many years ago by Professor Marsh and more recently recorded from Japan. The Japanese species is much more specialized and of larger size than the forms occurring on the Oregon and California coasts, which points to a general migration from east to west, that is, from the Orient to the Pacific coast of North America.

From this series of papers we are able to draw up the following table showing the principal distribution of the species of mammals in the descending order of the deposits in Japan:

Postpliocene of Shôzu-shima (Sanuki): *Stegodon sinensis, S. orientalis, Loxodon antiquus namadicus, Bison occidentalis, Cervus* (*Sika*) cf. *nippon.*
Upper Pliocene of Ikadachi-mura (Omi): *Stegodon sinensis, S. orientalis, Buffelus* sp.
Middle Pliocene of Tomuro (Kaga): *Elephas auroræ.*
Upper Miocene of Kuji (Hitachi): *Stegodon* cf. *latidens.*
Middle Miocene of the Provinces of Teshio, etc.: *Desmostylus japonicus.*
Lower Miocene of the Province of Mino: *Trilophodon* cf. *angustidens, Teleoceras* sp., *Amphitragulus minoënsis.*

The present researches of Doctor Matsumoto on the rich Fayûm collections of the American and British Museums have enabled him to draw an important distinction in northern Africa between the true forest-living mastodons, which appear to be directly descended from the genus *Palæomastodon* of the Fayûm, and the long-jawed mastodons, which appear to be directly descended from *Phiomia* of the Fayûm. This interesting discovery, which was partly anticipated in Doctor Andrews's own papers, enables us to trace the American mastodon far back into Upper Eocene times of northern Egypt.

In this connection may be mentioned also a series of five papers[2] by the present reviewer on the "Evolution, Phylogeny, and Classification of the Proboscidea" which have appeared successively since 1918. The writer is attempting to give an iconographic revision of the entire group of proboscideans, including the progenitors of Africa and Eurasia and the highly developed descendants of North and South America, which together make up the most remarkable family history of which we have record.

In 1900 Osborn predicted that the source of the mammalian order of the Proboscidea would probably be discovered in Africa. In 1901 Beadnell and Andrews revealed, through the Geological Survey of Egypt, the rich fauna of the Fayûm, southwest of Cairo, in which were found the remains of three proboscidean genera, named by Andrews *Mœritherium, Palæomastodon, Phiomia,* and confirmed by subsequent exploration and research to be the oldest proboscideans thus far known. Animals similar to *Mœritherium* and *Phiomia* have since been reported by Pilgrim in southern Asia. These animals are

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[2] The first paper in this series is entitled " A Long-jawed Mastodon Skeleton from South Dakota and Phylogeny of the Proboscidea," *Bull. Geol. Soc. Amer.*, XXIX, March, 1918; the second paper, "Evolution, Phylogeny, and Classification of the Proboscidea," *Amer. Mus. Novitates* No. 1, January 31, 1921 (Osborn, 1921. 515); the third paper, "First Appearance of the True Mastodon in America," *Amer. Mus. Novitates* No. 10, June 15, 1921; the fourth paper appears in the *Bulletin* of the Geological Society of America, under the title "Evolution, Phylogeny, and Classification of the Mastodontoidea"; the fifth paper, "Adaptive Radiation and Classification of the Proboscidea," was read before the National Academy of Sciences, April 26, 1921. The present is the sixth paper. The Iconographic Type Revision will form one of the Memoirs of the American Museum of Natural History.

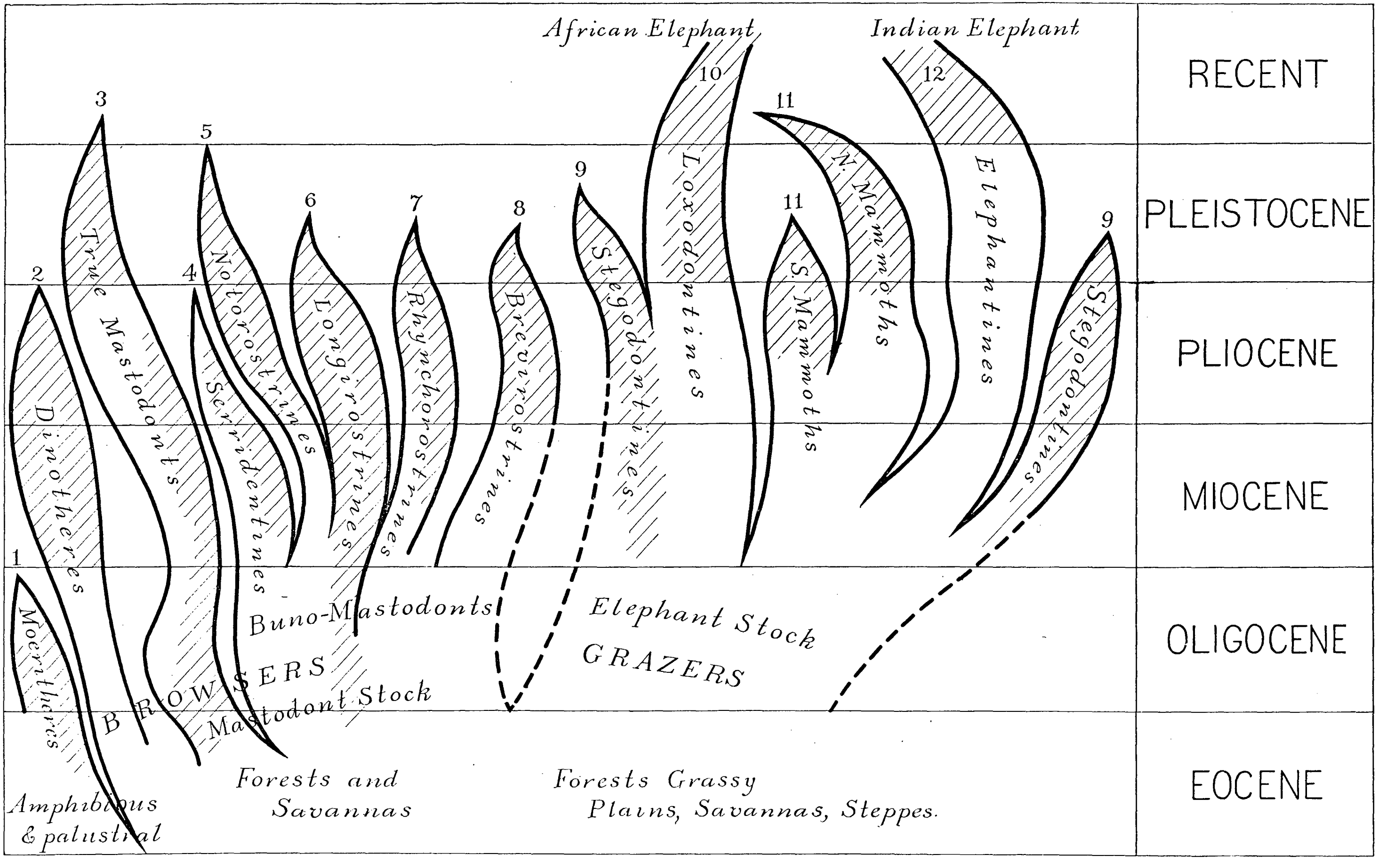

FIG. 1. Diagram showing the present theory as to the adaptive radiation of the Proboscidea. June, 1921.

now found to belong respectively to three distinct lines of the Proboscidea, namely, the mœritheres, the true mastodonts, the long-jawed bunomastodonts, as indicated in black on the accompanying diagram. They point, however, to a long antecedent origin and radiation. This is part of the evidence for an ancient adaptive radiation process by which it now appears that the proboscideans, like other hoofed mammals, were broken up into several great primary stocks way back in Eocene times, namely:

An *amphibious* stock, adapted to rivers and swamps, of limited migration (= *Mœritherium, Dinotherium*).
A *mastodont* stock, adapted to forests and savannas, of wide migration (= mastodonts, trilophodonts).
A *stegodon-elephant* stock, adapted to southern forests, to grassy plains, to savannas and steppes, of wide migration (= *Stegodon, Loxodon, Elephas*).

These primary stocks gave off from two to six branches each, so that the Proboscidea as a whole are not two branched (*i.e.*, mastodonts and elephants), as formerly supposed, but many branched or *polyphyletic*. The forest and savanna browsers and the grazers of the plains and steppes were the long distance travelers and from an African or Asiatic center in Eocene times they reached in the Middle and Upper Miocene all the continents of the world except Australia, while the amphibious forms remained in Africa and southern Eurasia. Certain of these branches, like the true mastodons, are of very great geologic antiquity. Intelligent, independent, well defended, resourceful, adaptive, we find eleven very distinct branches of proboscideans persisting into Upper Pliocene times, five of the least hardy of which became extinct during the colder conditions of the Lower Pleistocene. The known lines of evolution are shaded on the accompanying diagram; the unknown are left in white. The theoretic adaptive radiation may be expressed in a formal classification as follows:

Amphibious and swamp-living stock

- I. MŒRITHERIOIDEA (Mœritheres)
  - 1. Mœritheriini,[3] amphibious or swamp-living forms known in the Upper Oligocene of Africa.
- II. DINOTHERIOIDEA (Dinotheres)
  - 2. Dinotheriini,[4] large amphibious forms frequenting the rivers of southern Eurasia throughout the Miocene to the close of the Pliocene.

Forest and savannà grazers

- III. MASTODONTOIDEA (Mastodonts and Bunomastodonts)
  - Mastodontidæ or "true mastodonts," including the subfamilies
    - 3. Mastodontinæ, springing from *Palæomastodon* of the Oligocene of North Africa, and terminating with *Mastodon americanus* of the Pleistocene forests of North America; grinders lophodont, lacking trefoils.
    - 4. Serridentinæ,[5] first known in the Middle Miocene of France and Switzerland, spreading over into India and North America; lacking the trefoils.
  - Bunomastodontidæ, the bunomastodonts, springing from forms similar to the *Phiomia* of North Africa and separating into four main divisions:
    - 6. Longirostrinæ, typical long-jawed bunomastodonts arising in North Africa (*Phiomia*), spreading all over southern Europe, Asia, and North America.
    - 5. Notorostrinæ, a special branch entering the Andean region of South America and spreading over the South American continent, distinguished by the loss of the lower tusks and the abbreviation of the jaw.
    - 7. Rhynchorostrinæ, beaked bunomastodonts, known only in the southern United States and northern Mexico, with powerful downturned upper and lower tusks.
    - 8. Brevirostrinæ, short-jawed bunomastodonts, which imitate both the true mastodonts and the elephants in the abbreviation of the lower jaw and the early loss of the inferior tusks.

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[3] Herluf Winge, 1906, p. 172.

[4] *Ibid.*

[5] It is a question whether this subfamily is nearest the Mastodontidæ, with which its members are generally placed by European paleontologists.

These animals wandered all over Europe, Asia, and western North America.

IV. ELEPHANTOIDEA (the Elephant stock)

9. Stegodontinæ, the original members of which were doubtless ancestral to all the higher elephants, persist as an independent branch into the Lower Pleistocene of eastern Asia.
10. Loxodontinæ, embracing the great African division of the elephants beginning with varieties of the *Loxodon antiquus* of the Upper Pliocene, which wandered all over southern Eurasia and radiated widely over Africa.
11. Mammontinæ, including (*a*) the Southern Mammoths (*Elephas planifrons* of India and *E. meridionalis* of Europe), from which is derived *E. imperator* of North America, and (*b*) the Northern Mammoths, which probably include *E. columbi* and the widespread *E. primigenius* of the northern steppes; (?) tetradactyl pes.
12. Elephantinæ, the true elephants (*E. indicus* of India), which do not appear until the Upper Pleistocene; pentadactyl pes.

This twelve-fold branching of the proboscideans is similar to the adaptive radiation which the author has traced in the evolution of the horses, of the rhinoceroses, and of the titanotheres, carrying the fundamental lines of separation back to the Middle Miocene as the most recent date, and to the Middle or Lower Eocene as the most remote date. It will be observed from the diagram (Fig. 1) that the shaded areas represent those proboscidean phyla of which remains have been discovered. The large unshaded area includes the entire Oligocene, Miocene, and Lower and Middle Pliocene history of the Elephantidæ which is still unknown but which is likely to be revealed at any time by discoveries both in Africa and in central Asia. A very striking fact is that the early member of the Elephantoidæ, the *Elephas planifrons* of the Upper Pliocene of India and the apparent ancestor of the mammoths, is now antedated in geologic time and in its transitional structure by the *Elephas auroræ* (*i.e.*, of the rising sun region) of Japan.